Report from the Biology and Ecology Working Group

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INTRODUCTION

The Working Group was charged with evaluating the life history characteristics and the genetic makeup of *Acropora* populations and how these factors influence the success of these species, including their ability to persist under varying environmental conditions and their ability to recover following a biotic or abiotic disturbance. The group was also charged with evaluating the importance of these species in terms of essential habitat for other species, reef construction and other factors. Finally, the group was asked to discuss the most appropriate conservation strategies to enhance recovery, based on the biology and ecology of these species.

1. The Role of Acroporid Corals as Essential Reef Habitat

Acroporid corals play a major role within reefs of the Caribbean reef communities by providing the geological, physical, and biological foundation for the development of numerous shallow reef communities (e.g., Adey, 1975; Hubbard et al., 1994; Aronson and Precht, 1997). Their recent decline (up to 95% mortality at some locations) within the last three decades has highlighted their critical ecological role within reefs where they have historically supported a very productive reef community that depends on these species directly for food and refuge (Table 1). Coring studies have documented the geologic importance of *Acropora* spp. as reef builders (e.g., Hubbard et al., 1994; Aronson et al., 2002). The fast growth rates of Acroporid species as well as the rapid accretion rates of *Acropora*-dominated reefs has allowed populations of these corals to keep up with sea level rise through the Holocene (although populations were drowned and replaced by other coral species at many locations) (Gladfelter et al., 1978).

The role of Acroporids as structural (or foundation)[1] species within reef communities has been well documented. Lirman (1999) showed an association between the distribution of fish schools composed mainly of grunts and snappers and *Acropora palmata* colonies. These schools, which often remain in the same location for extended periods, utilize the topography offered by the elkhorn branches as diurnal refuge. Fish aggregations not only composed a large portion of fish biomass on the reefs surveyed, but they could also contribute to the flux of materials from surrounding vegetated areas to the reef through their daily feeding migrations (Meyer et al., 1983; Parrish, 1987). The excretory products of these fish schools can also contribute to the productivity of corals and algae in the area surrounding their refuge (Nelson, 1985; Bray et al., 1986), and even stimulate coral growth by providing nitrogen supplements (Meyer and Shultz, 1985 a, b). Direct associations between Acroporid corals and other reef fishes such as damselfishes, squirrelfish, glassy sweepers, and many others have also been reported (e.g., Emery; 1973; Clarke, 1977; Itzkowitz, 1977; Gladfelter and Gladfelter, 1978; Waldner and Robertson, 1980; Meyer et al., 1983; Meyer and Shultz, 1985a, b; Thompson et al., 1990; Williams, 1991, Clarke, 1996). In addition, Acroporid corals provide essential habitat (i.e., food, refuge, recruitment habitat) for turtles, lobsters, crabs,

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[1]Species of large effect fall into two general categories: 1) structural or foundation species, which provide most of the three-dimensional architecture in which other species find shelter and food; 2) keystone species, which by virtue of their high rates of consumption and their generalized diets, exercise disproportionate control over the distributions, population sizes, activities, and adaptive characteristics of many other species (Vermeij, 2001).

echinoids, and gastropods. These documented relationships suggest clearly that changes in the extent and composition of *Acropora* spp. populations can result in significant changes in associated reef fauna.

Resolution: *The structural and ecological roles of Acroporid corals in the Caribbean are unique and can not be filled by other coral species. Their rapid accretion rates and structural complexity are unmatched. The loss of these characterstics will likely result in a significant loss of reef function and structure. At present, there is no indication that any other Caribbean coral species can replace the important role that Acroporid corals play within reef communities of the region.*

2. Disturbance and Acroporid Populations

At the recent *Acropora* Workshop, members of the biology and ecology working group discussed the response of Acroporid corals to multiple stressors. Based on published reports and personal observations, the patterns of susceptibility, resistance, and resilience of these important coral species to stress are summarized in Table 2. Within this table, both documented and potential sources of disturbance are included to highlight the possible impact of future disturbance on the recovery of Acroporid corals, and to indicate areas where active management practices can play a role in mitigating the impacts of stressors.

Resolution: *Two sources of disturbance, diseases and storms, were identified as the main contributors to the regional decline of Acropora spp. In addition, sources of mortality such as chemical pollution and space competition from excavating sponges, were identified as "emerging issues" where more research is needed to fully predict their impacts.*

3. Coral Diseases

The drastic decline in the abundance and cover of Acroporids in the Caribbean due to white-band disease (WBD; a presumed bacterial infection specific to this group) has been documented by Gladfelter (1982), Bythell and Sheppard (1993), and Aronson and Precht (2000, 2001). Unlike other sources of disturbance with mainly localized impacts such as hurricanes, the impacts of WBD on Acroporid corals have been region-wide (reviewed by Aronson and Precht, 2000). This unprecedented decline has changed the structure of shallow coral reefs dramatically. The replacement of Acroporids by other coral species and/or macroalgae has modified historical reef zonation patterns once defined by the dominance of *Acropora palmata* at shallow fore reefs (0-5 m) and *A. cervicornis* at intermediate depths (5-25 m) (Geister, 1977; Adey, 1978; Aronson and Precht, 2000).

Resolution: *White-band disease, which affects both Acropora palmata and A. cervicornis, is believed to have been the principal cause of mortality in these species throughout the Caribbean region in the past two decades.*

4. Hurricanes and Tropical Storms

The impacts of hurricanes and tropical storms on Acroporid species have been summarized by Harmelin-Vivien (1994), Lirman (1997), Aronson and Precht (2000), and others. Their branching morphology and their location within shallow, wave-exposed areas of reefs make Acroporids highly susceptible to physical disturbance. Fragmentation and dislodgment of *Acropora* spp. were reported after Hurricanes Hattie (Stoddart, 1963, 1965; Zea et al., 1998), Edith (Glynn et al., 1964), Gerta (Highsmith et al., 1980), Allen (Woodley et al., 1981), David and Frederic (Rogers et al., 1982), Hugo (Gladfelter,

1991), Joan (Zea et al., 1998), Gilbert (Kobluk and Lysenko, 1992; Jordan-Dahlgren and Rodriguez-Martinez, 1998), and Andrew (Lirman and Fong, 1996, 1997), as well as after Tropical Storms Bret (Van Veghel and Hoetjes, 1995) and Gordon (Lirman and Fong, 1997).

The direct and indirect impacts of storms on Acroporid populations can be significant in terms of tissue mortality, fragmentation, and colony dislodgment. However, the ability of *Acropora* spp. to form new colonies from fragments (e.g., Bowden-Kerby, 1997; Lirman, 2000), together with the reportedly low success of sexual recruitment in this species (Dustan, 1977; Bak and Engel, 1979; Hughes and Jackson, 1980, 1985; Rylaarsdam, 1983; Rosesmyth, 1984), suggest a strong connection between storm disturbance and persistence of this group.

Resolution: *Acroporid corals may require a certain storm frequency to be able maintain and expand populations through asexual recruitment when sexual recruitment is limited. However, a frequent occurrence of storms, or a particularly intense hurricane may impact colony and fragment survival.*

5. Reproductive Characteristics of Acroporids
A. Sexual Reproduction

Coral colonies exist as modules (ramets) capable of surviving alone or in small groups. The sum of all ramets derived from a single zygote constitutes the coral's genet, which, unlike aclonal organisms, can exist as independent units that may experience diverse environmental conditions (Coates and Jackson, 1985; Heyward and Collins, 1985; Harper, 1985). *Acropora palmata* and *A. cervicornis* are broadcast spawning hermaphrodites with one reproductive cycle per year (Szmant, 1986; Steiner, 1995). Egg and sperm bundles are released into the water column for external fertilization. The positively buoyant gametes float to the surface where they can remain viable for up to 8 hrs. Histological work and nightly spawning observations indicate that the predicted spawning time for *A. palmata* is 2-4 nights after the full moon in Aug/Sept while *A. cervicornis* spawning has been observed 2–7 days after the full moon in July/August (Steiner, 1995; Szmant, pers. obs. Vargas-Angel & Thomas 2002, pers. obs). However, *Acropora* spp. appear to be much less predictable in their spawning activity than other well-studied groups (e.g., *Montastraea* spp.). For example, a histological study by Jaap et al. (unpublished) of *A. palmata* in the late 70's-early 80's showed no gonad development during 2 of the 5 yr study while all other species examined were consistent across years. Also, no *A. palmata* spawning was observed during the night 2-4 window in Aug 2000 in Key Largo, FL and in La Parguera, Puerto Rico (M. Miller and Szmant, pers. obs.). In Aug 2001, *A. palmata* spawning was observed in the Florida Keys but on night 5 after the full moon, one night "late" (M. Miller, pers. obs.).

A. palmata spawn has been successfully raised to settlement in laboratory and field enclosures (Szmant & M. Miller, unpubl). In the laboratory, competence of planktonic larvae was documented at 5 days. Zooxanthellae, perhaps taken up from conditioned reef rubble offered as settlement substrate, were observed in the tentacles of the initial settled polyps. However, the mechanism of zooxanthellae transfer or uptake is unknown at present. Successful cultures from spawn to settlement were made at Key Largo Dry Rocks, Florida in 1996 and 1997 (Szmant, pers. comm.).

Resolution: *For Acroporid corals, which exhibit reportedly sporadic or limited sexual recruitment, asexual reproduction can play a major role in maintaining local populations. However, as population abundance decreases or disturbance patterns increase to the point where remaining coral populations are no longer able to survive and propagate by asexual means, the relative importance of sexual reproduction and recruitment increases.*

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While the energetic investment in gamete production and release is apparent, sexual recruits of Acroporids were absent, or present in very low numbers, in several settlement studies, leading to the generally accepted conclusion that these species exhibit low levels of sexual reproductive success (e.g., Dustan, 1977; Bak and Engel, 1979; Hughes and Jackson, 1980, 1985; Rylaarsdam, 1983; Rosesmyth, 1984; Knowlton et al., 1990). Although this may still be true, researchers at the *Acropora* workshop believe that the observed patterns of limited sexual recruitment success may not represent necessarily a life-history characteristic of this group. In fact, it was concluded that the documented patterns may be an artifact of: 1) the methods used in these studies (i.e., settlement tiles that may not offer the appropriate settlement substrate for Acroporids), 2) the timing of most of these studies (i.e., after the onset of the regional decline of Acroporids when adult densities were drastically reduced), and 3) the duration of these studies (i.e., never long enough to capture stochastic settlement events).

Resolution: *Anecdotal evidence and observations made by reef researchers at several locations throughout the region indicate that both A. palmata and A. cervicornis do indeed recruit sexually onto reefs and that in several instances (e.g., Tague Bay Reef and other north shore reefs of St. Croix, USVI, Gladfelter, pers. obs.) populations that have experienced major declines (< 90%) are presently showing signs of recovery from newly settled sexual recruits.*

B. Asexual reproduction

In contrast to the limited information available on the patterns of sexual reproduction and recruitment for Acroporid corals in the region, patterns of asexual reproduction through fragmentation are well documented, and several consequences of asexual reproduction have been suggested for corals (Table 3). The organization of coral colonies into modules allows the biomass of a genotype to increase beyond the mechanical limits of individual colonies by the formation of tissue isolates and fragments (Jackson, 1977; Hughes et al., 1992). When growth-rates decline with increasing colony size (e.g., Maragos, 1974; Loya, 1976; Hughes and Jackson, 1985), fragmentation may help maintain high growth-rates by "pruning" colonies, creating new, smaller units. The larger size of fragments compared to sexually produced coral planulae may result in higher survivorship after recruitment (Jackson, 1977) and the colonization of areas not suitable for larval development, such as soft-bottom habitats (Highsmith, 1982; Heyward and Collins, 1985). Within populations that experienced recent storms, *A. palmata* fragments can comprise a large percentage of ramets as well as cover a large percentage of the bottom (Highsmith, 1982; Lirman and Fong, 1997). Similarly, demographic studies of *A. cervicornis* distributed along the coastal waters off Fort Lauderdale, Florida revealed that fragments can comprise over 40% of the staghorn coral population at the study sites (Thomas et al., 2000; Vargas, unpub. results).

Asexual propagation through fragmentation is often concentrated in time and fragmentation followed by fragment stabilization can result in a rapid increase in ramet abundance and coral cover, leading to space monopolization by fragmenting coral species (Lirman and Fong, 1997; Lirman 2000a). Unlike sexual reproduction, which is highly seasonal for *Acropora palmata* and *A. cervicornis* (Szmant, 1986), fragmentation can take place year-round. Similarly, successful asexual reproduction of colonies can take place even at low colony abundance and does not require multiple colonies for gamete concentration and fertilization.

Despite these potential benefits of fragmentation, there are negative consequences associated with this process that need to be considered (Table 3). The final outcome of fragmentation may be a total increase

in biomass after a period of growth (Clark and Edwards, 1995), but initial tissue losses and the reduction in colony size can produce negative consequences as colony size in cnidarians has been directly associated with survivorship, growth, and reproduction (e.g., Connell, 1973; Loya, 1976; Highsmith, 1982; Jackson, 1985; Karlson, 1986, 1988; Hughes and Connell, 1987; Lasker, 1990; Babcock, 1991; Hughes et al., 1992). The immediate tissue losses after fragmentation can be significant. Fragment survivorship is influenced by the type of substratum where fragments land. In Florida, fragments that landed on top of live elkhorn colonies fused to the underlying tissue rapidly and showed no signs of mortality. In contrast, fragments placed on sand lost 58% of their tissue within the first month and 71% after four months (Lirman, 2000a). Similarly, the survivorship of *A. cervicornis* fragments is strongly determined by the type of substratum and fragment size (Bowden-Kerby, 1997; Vargas, unp. results).

During fragmentation, skeletal lesions are formed on both the fragments and the source colonies, and the recovery of lesions has been shown to be a considerable energetic drain on the damaged colonies (Meesters 1996, 1997). Furthermore, since linear growth can not resume until lesions are recovered and axial polyps form, lesions can also reduce the growth rates of damaged colonies (Lirman, 2000b). Similarly, the colonization of lesions by bioeroders can weaken coral colonies (Hernandez-Ávila et al., 1977; Mitchell-Tapping, 1983).

Severe fragmentation, as commonly observed after storms, may limit future sexual reproduction by reducing the biomass of colonies and shifting the energy allocation of damaged colonies from reproduction to stabilization and regeneration (Van Veghel and Bak, 1994; Van Veghel and Hoetjes, 1995; Hall and Hughes, 1996). Lirman (2000a) showed that hurricane-damaged *A. palmata* colonies and fragments on Florida reefs did not produce gametes until five years after the initial disturbance. Also, the size and weight of fragments may limit their dispersal range (Williams, 1975; Wulff, 1985; Jackson, 1986), slowing the recovery of damaged areas where the cover of adult colonies has been reduced significantly (Aronson and Precht, 2001; Precht et al., 2002). In such cases, recovery will depend on the recruitment of sexual propagules produced in distant, undisturbed areas (Connell and Keough, 1985).

Resolution: *The information available on patterns of asexual propagation has shown that, under the right environmental conditions, fragmentation followed by fragment stabilization, survivorship, and regrowth can provide an efficient mechanism for maintaining and expanding Acroporid populations. However, while fragmentation followed by fragment stabilization and growth may have been sufficient to maintain and expand Acroporid populations in the past, recent patterns of regional decline have increased the reliance of these species on sexual recruitment as a means of establishing and sustaining populations. Accordingly, the regional recovery of Acroporid populations will depend largely on the future success of sexual recruitment.*

6. Genetic Status of *Acropora* Populations

Acroporid populations showed a significant Caribbean-wide decrease in the 1980s attributed, at least in part, to the epizootic white-band disease, a disease specific to this genus (Antonius 1981; Gladfelter 1982; Peters 1993; Aronson and Precht, 2001). Moreover, the branching Acroporids are especially susceptible to the physical damage caused by storms that have resulted in significant additional losses

(e.g., Woodley et al., 1981). Declines of up to 95% attributed to these and other stressors have been observed at locations throughout the region where Acroporids were once the dominant on shallow reef zones.

Resolution: *In light of the recent drastic decline of these critical structural (foundation) species, it is important that we understand the influence of disturbances on the genetic composition and genetic variability within and among Acroporid populations. Furthermore, faced with the uncertainty about their recovery and long-term status it is important to determine whether these disturbances have modified underlying genetic variability, favoring locally adapted, disturbance-resistant populations. This information will be crucial to: 1) evaluate, based on present genetic structure, the potential impact of future disturbances, and 2) determine, based on prior genetic exchange, the recovery capability of local populations from remaining regional sources of propagules. Similarly, information on the clonal structure of the populations will aid in the decision making process on marine reserves and management plans by identifying specific locations and populations at risk based on factors such as genetic isolation and genetic structure.*

Acropora spp. in the region reproduce both sexually and asexually. Asexual reproduction, which is a common reproductive and propagative strategy in this group (e.g., Tunnicliffe, 1981; Highsmith, 1982; Lirman, 2000a), leads to the multiplication of a genotype and results in an assemblage of genetically identical individuals or clones (Carvalho, 1994). Asexual reproduction per se has no effect on allelic or genotypic frequencies in populations. It does not allow for genetic segregation and recombination, however, and so preserves the effects of selection, genetic drift, or founder effect on genetic diversity. In addition, *A. palmata* and *A. cervicornis* reproduce sexually by releasing egg-sperm bundles in the water (broadcast spawning; Szmant, 1986; Steiner, 1995). The pelagic life stage provides the opportunity for long-distance transport of larvae with the surface currents (Sheltema, 1977; Crisp, 1978).

The dominance of asexual reproduction combined with broadcast spawning may have significant implications on the damage and recovery patterns of Acroporid populations and has led to a prediction of small effective population size and low genotypic diversity within Acroporid populations. As early as 1983, Bak (1983) hypothesized that high asexual reproduction rates can lead to low genotypic diversity so that Acroporids are more susceptible to disease compared to non-branching species.

The effective population size (i.e., the number of breeding individuals) reaches a maximum when all genets contribute to the next generation. Acroporid populations are expected to have a small effective population size if both fertilization success of spawned gametes and the recruitment of larvae are highly stochastic and dependent upon local conditions. By chance, only a few individuals might contribute a large number of offspring to the next generation (sweepstake effect; Hedgecock, 1994a, b). Once colonies become rare, the distance between them might limit fertilization success (Allee effect) even further. This is important for already declining Acroporid populations because small effective population sizes are far more prone to extinction due to demographic stochasticity, reduction in gene diversity, or accumulation of deleterious mutations (Grosberg and Cunningham 2000). The consequences of asexual reproduction on genotypic diversity depend largely on the frequency of sexual recruitment and genet longevity. Empirical and theoretical studies have suggested that genotypic diversity at a local scale might decrease over time through elimination of genets by intraspecific competition or stochastic effects. In contrast, genotypic diversity might remain high if sexual recruits, however rare, have a long life span after establishment (McFadden, 1997).

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Resolution: *The scientific capability to assess the potential for recovery of Acropora spp. populations by sexual propagation of surviving populations is seriously impaired at present by the general lack of knowledge of the different aspects of this process. This was identified as a key research area where efforts need to be allocated in the future to determine: 1) spatial and temporal patterns of gamete formation and release, 2) size-stage thresholds for gamete production, 3) within and among colony variability in gamete production, 4) fertilization patterns, 5) transport and duration of larval stages, 6) larval survivorship patterns, 7) settlement requirements and preferences of coral planulae, and 8) early survivorship and growth of sexual recruits.*

In an early study to detect clonal identity with Acroporid populations, Neigel and Avise (1983) utilized self-recognition analyses to show that: 1) *A. cervicornis* clones do not extend further than 20m, 2) one clone may dominate areas of $10m^2$, and 3) clones are generally spatially discrete with tight boundaries. However, the genetic basis of tissue compatibility has since been challenged by studies showing fusion of electrophoretically distinct ramets. Analysis of protein (allozyme) and DNA markers show patterns from dominantly asexual to dominantly sexual reproduction in the Scleractinia. Even within the same species, contrasting reproductive behavior over large geographical scales is not exceptional (Harrison and Wallace, 1990).

The genetic structure of *A. palmata* populations is currently under investigation (Baums, in progress). Both clonal structure and reef connectivity will be estimated by combining highly variable, mendelian markers (microsatellites) with a nested sampling approach on a variety of spatial scales. Genetic analyses conducted by Vollmer and Palumbi (2002) clearly shows that the three Caribbean *Acropora* comprise a natural hybridization system with *A. prolifera* being a morphologically variable, first generation hybrid of *A. palmata* and *A. cervicornis*. While the parent species *A. cervicornis* and *A. palmata* are genetically distinct, rare backcrossing of *A. prolifera* with *A. cervicornis* allows for limited mitochondrial and nuclear introgression (Vollmer and Palumbi, 2002). As a result, the genome of *A. cervicornis* may be sprinkled with *A. palmata* genes. An important distinction for the status and conservation of *A. cervicornis* is that the genetic data show it is a distinct species or genetic lineage, despite its introgression. One avenue of their on-going research is to assess the potential role of genetic introgression on the relative fitness of various *A. cervicornis* genotypes. In addition, with the genetic markers used for the hybridization work, they are also characterizing levels of genetic diversity and population structure of *A. cervicornis* throughout the Caribbean. Preliminary data suggests there is population structure among islands, and potentially even over small spatial scales (ca. 20kms), and varying degrees of genetic diversity within local populations. In Puerto Rico, for example, they are finding surprisingly high levels of genetic diversity at some sites (ca. 1 genotype per 5m), while other sites appear to be dominated by a single clone.

Resolution: *The preliminary results highlighted here can have important conservation implications – namely, each coral population should be considered individually and any conservation strategy (esp. transplantation studies) should take into account preserving 'meaningful genetic diversity'.*

Table 1. Contribution of Acroporid corals to the reef communities of the Caribbean region

- •• REEF-BUILDING / FRAMEWORK CONSTRUCTION
- •• CARBONATE DEPOSITION
- •• TOPOGRAPHICAL RELIEF / COMPLEXITY
- •• ESSENTIAL HABITAT FOR ASSOCIATED REEF SPECIES
- •• PROTECTION FROM EROSION / WAVE ACTION
- •• BIODIVERSITY
- •• MICROHABITAT DIVERSITY
- •• AESTHETICS
- •• SCIENTIFIC VALUE
- •• EDUCATIONAL VALUE
- •• RECREATIONAL VALUE
- •• COMMERCIAL VALUE

Table 2. Stressor-response characteristics of Acroporid corals in the Caribbean. The information included in this table is based on published reports and expert opinion recorded at the Caribbean Acroporid Workshop, April 16-18, 2002, Miami. While the information provided here emphasizes documented responses of Acroporid corals to stressors, it is recognized that stressors known to affect other coral species may influence Acroporids in similar fashion even when data to test this are not available. Similarly, while the direct effects of individual stressors are emphasized here, it is recognized that many stressors have indirect and synergistic effect pathways that need to be considered. Lastly, while the lethal effects of stressors are emphasized here, it is recognized that many of these stressors commonly have sub-lethal effects such as reduced calcification, growth, reduced reproductive output, and reduced recruitment that can have important consequences on the long-term survivorship of these species. Emerging issues are recognized as potentially important stressors for which limited information is available and more research is needed. Susceptibility: High, Medium, Low; Effects: Lethal (whole colony mortality), Partial (patchy tissue mortality), Minimum; Spatial Extent: Regional, Local; Resilience (i.e., time required to recover from impacts): High, Medium, Low; Effect Pathway: Direct, Indirect (mechanism). * Although bleaching is commonly recognized as a coral response to stress, it is included in this list due to the potential role of bacteria in causing this response.

Table 2. Stressor-response characteristics of Acroporid corals in the Caribbean.

STRESSORS	Susceptibility	Effects	Spatial Extent	Resilience	Effect Pathway
Diseases / Pathogens					
White Band Disease	High	Lethal	Regional	Low	Direct
Patchy Necrosis / White Pox	High	Partial	Local - Regional	Medium - High	Direct
Bleaching *	Low - High	Partial - Lethal	Local - Regional	Low	Direct
Physical Damage					
Storms	High	Minimum - Lethal	Local - Regional	Low - High	Direct
Groundings / Anchor Damage	Medium - High	Minimum - Lethal	Local	Medium - High	Direct
Competitors					
Snails (*Coralliophila abbreviata*)	Low - High (depend on population	Partial - Lethal	Local	Depends on extent of predation	Direct
Fireworms (*Hermodice carunculata*)	Low - Medium	Partial	Local	Medium	Direct
Damselfishes	Low - Medium	Partial	Local	Medium	Direct + Indirect (algal competition)
Parrotfish (*Sparisoma viride*)	Low - Medium (depend on population	Partial	Local	Low	Direct + Indirect (algal competition)
Bioeroders	Low - Medium	Partial	Local	Medium - High	Direct
Sea Urchins	Low	Minimum	Local	High	Direct + Indirect (fragmentation)
Clionid Sponges	High	Lethal	Local - Regional	Low	Direct
Macroalgae	Medium	Partial - Lethal	Local - Regional	Medium	Direct + Indirect (recruitment)
Temperature	Unknown	Lethal at extremes	Local-Regional	Low at extremes	Direct + Indirect (bleaching)
Irradiance	Unknown	Unknown	Local - Regional	Unknown	Direct (UV) + Indirect (bleaching)
Reduced Water Motion	Medium - High	Lethal if persistent	Local	Unknown	Direct + Indirect (bleaching)
Siltation	Medium	Partial	Local	Medium - High	Direct + Indirect (recruitment)
Salinity	Unknown	Unknown	Unknown	Unknown	Unknown
Nutrients	Unknown	Unknown	Local	Unknown	Direct + Indirect (recruitment, algal competition, bioerosion)
Solid Waste	Low	Partial	Local	Medium - High	Direct
Chemicals	Unknown	Unknown	Local - Regional (Emerging issue)	Unknown	Direct
Increased CO_2	Unknown	Unknown	Regional (Emerging issue)	Unknown	Indirect (calcification)

Table 3. Potential benefits and consequences of fragmentation and asexual reproduction of Acroporid species in the Caribbean.

POTENTIAL BENEFITS OF FRAGMENTATION

- RAPID SPACE MONOPOLIZATION
- REPRODUCTION IN ISOLATION (NO CROSSING)
- HIGH SURVIVORSHIP OF PROPAGULES
- REDUCED SEASONALITY
- INCREASED LOCAL ABUNDANCE
- INCREASED BIOMASS (AFTER REGROWTH)
- COMPETITIVE ADVANTAGE
- EXPANDED HABITAT SUITABILITY
- REEF EXPANSION / CREATION OF PRIMARY SPACE
- AVOIDANCE OF SIZE / SHAPE LIMITATIONS
- AVOIDANCE OF SENESCENCE
- INCREASED GENET SURVIVORSHIP

POTENTIAL CONSEQUENCES OF FRAGMENTATION

- TISSUE LOSSES
- LESION FORMATION
- REDUCED AVERAGE SIZE OF RAMETS
- REDUCED GROWTH RATES
- INCREASED MORTALITY RATES
- INCREASED SUSCEPTIBILITY TO STRESSORS
- INCREASED BIOEROSION
- REDUCED SEXUAL REPRODUCTIVE OUTPUT
- REDUCED PROPAGATION CAPABILITIES
- REDUCED GENETIC DIVERSITY